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**FACTORS INFLUENCING THE SIZE, SHAPE
AND PHYSICAL CONSTITUTION OF THE
EGG OF THE DOMESTIC FOWL**

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AN ABSTRACT OF A THESIS SUBMITTED IN PARTIAL FULFILLMENT
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FACTORS INFLUENCING THE SIZE, SHAPE AND PHYSICAL CONSTITUTION OF THE EGG OF THE DOMESTIC FOWL.*

MAYNIE R. CURTIS.

In a study of the physiology of reproduction in the domestic fowl one must soon recognize the fact that the number of eggs produced is only a rough measure of the reproductive activity for the eggs produced are not all equivalent. The complicated physiological processes involved in the production of an egg are so influenced by both heredity and environment that they result in quite unequal products. Eggs differ greatly in every character. The scientific and economic importance of differences in size and quality is obvious.

Investigations on inheritance in poultry have been in progress at this laboratory for several years. In this work the eggs of about two hundred hens of one breed are handled individually each season. The variation in these eggs is very great. The four following facts in regard to it are apparent.

I. The eggs of different individuals of the same strain vary in size, shape, color and markings.

* This paper is an abstract, setting forth the more important results and conclusions, of an extended paper by the same author, published under the following title: "A Biometrical Study of Egg Production in the Domestic Fowl. IV. Factors Influencing the Size, Shape and Physical Constitution of Eggs," in *Archiv fuer Entwicklungsmechanik der Organism* (Roux). Bd. 39, pp. 217, 1914. The three previous papers in the series are:

Pearl, R. and Surface, F. M. A Biometrical Study of Egg Production in the Domestic Fowl. I. Variation in Annual Egg Production, U. S. Department of Agr., Bur. of Animal Industry, Bul. 110, pp. 1-80, 1909. II. Seasonal Distribution of Egg Production. *Ibid.* pp. 81-170, 1911. III. Variation and Correlation in the Physical Characters of the Egg. *Ibid.* pp. 171—, 1914.

2. The eggs of an individual are more like each other than they are like the eggs of other individuals of the same strain.

3. In spite of this resemblance between the eggs of the individual they nevertheless show a certain degree of variation in all their characters.

4. The first eggs laid by the pullets are smaller than those laid by the same birds later.

An analysis of the factors underlying this individuality and variation in the quantitative characters of the egg offers a new point of attack in the study of the physiology of egg production. A statistical study was made of the quantitative characters of all of the eggs laid by twenty-two Barred Plymouth Rock birds during their first two laying years. These birds were all from the Maine Agricultural Experiment Station strain, the purity of which has been amply proven by breeding experiments.

This paper presents briefly the results of this investigation of the shape and size, both absolute and relative, and the proportion of parts of the successive eggs of each of these birds. It includes (a) a study of the individuality of the eggs of each bird and the variation among them; (b) a study of the relation of the individuality of the eggs to other facts known about the bird, such as body weight, relative size of the several visceral organs, age, number of eggs laid, and tendency to broodiness; (c) the variation in egg characters in relation to the age of the bird, the seasonal reproductive cycles and the intensity of the reproductive activity, including the grouping of the successive eggs into clutches and litters, the size of these groups and the position of the eggs within them.

THE INDIVIDUALITY OF THE EGGS OF EACH BIRD IN REGARD TO SHAPE, SIZE, AND SIZE AND PROPORTION OF PARTS.

It was not necessary to resort to mathematical calculation to demonstrate the fact that the eggs of the different individual birds used in this investigation varied considerably in respect to size and shape. This inter-individual variation was easily seen by comparing the eggs of the different individuals. The eggs of one bird were from one-fourth to one-third larger than

the eggs of one of the others. Some of the birds laid eggs which were long and narrow, others those which were short and broad. The eggs of some individuals were distinctly pointed, while those of others were not.

Not only was it possible to see this individuality by comparing the eggs of the different individuals laid at the same season, but by preserving some of the shells of the eggs of each bird at various seasons it was possible to see that the relative size and the shape of the eggs of a fowl are to a large extent permanent characteristics of the individual.

The present investigation deals primarily with the quantitative or measurable characters of the egg, but that the individuality of the different birds manifests itself also in certain qualitative characters is illustrated by a comparison of the color and markings of the eggs of the different birds.

This variation which is seen by a comparison of the eggs themselves is shown equally clearly by a comparison of the measurements of the characters. It is not confined to the externally visible characters (dimensions, shape and size) but extends to the size and the proportion of the parts which make up the egg.

A statistical analysis of the data shows the following points:

INTER-INDIVIDUAL VARIATION.

1. The characteristic eggs of the different individuals show variation in all egg characters.

2. They differ more in size than in shape, and they differ more in the amount of albumen and shell than in the size of the yolk.

3. There is a general correlation between the various characters of the egg. That is, when a bird's eggs are large they are both long and broad and contain a large yolk with a large amount of albumen and shell. The amount of yolk, however, is not *proportionately* large, so that the birds which lay large eggs lay eggs which have a relatively small percentage of yolk.

4. In spite of this general relationship the eggs of one individual may vary disproportionately in any one of the characters measured.

5. There is an evident individuality among the birds also in the amount of variation in the egg characters. The uniform.

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ity (or variability) of the egg characters of an individual tends to be general, but may manifest itself in different characters to quite different degrees.

6. A comparison of the relative degree of variation in the individual and in the race shows that in general the eggs of an individual resemble each other much more closely than do a random sample of the eggs of the same strain. The eggs of certain individuals, however, show a much higher percentage of the variation of the race than those of some of the other individuals. In certain egg characters there is a general tendency for the individual variation to approach more nearly the limits of the race variation than in other characters. Finally certain characters may display a variation relatively greater in a particular individual than in the race. This indicates that the egg characters are determined by an interaction of hereditary and environmental forces which may cause a particular character to reach or surpass the racial limits of variation within the eggs of one individual.

INTRA-INDIVIDUAL VARIATION.

The different degree of variation shown by the several egg characters in each individual is also clearly seen. The four following relationships between the degree of variation in the separate characters are clearly demonstrated, either by comparing the average individual variation for each character taking the group of birds as a whole, or by considering separately the several coefficients for each bird.

1. *The egg varies more in respect to weight of shell and weight of yolk than in respect to any of the other characters.* A few individuals show significant differences between the amount of variation in these characters. The eggs of some individuals vary more in respect to the one and some in respect to the other.

2. *Egg weight and albumen weight are about equally variable. They are decidedly less variable than shell weight and yolk weight and much more variable than either length or breadth.* The difference between the variation for these two characters is significant for very few individuals.

3. *Both length and breadth are much less variable than any of the weight characters of the egg.*

4. *The egg is more variable in length than in breadth.* In a few individuals the difference between the variation in these characters is not significant.

The following list arranges the egg characters in the order of their variability.

- } Egg weight.
- } Yolk weight.
- } Albumen weight.
- } Shell weight.
- Length.
- Breadth.

It is especially worthy of note that the variation coefficients for yolk and shell are much higher than for the whole egg, and the coefficient for albumen is at least as high. There must then be a compensatory variation among the parts. The data show also that the eggs of the breeding season have disproportionately large yolks and a consequent smaller percentage of albumen than the eggs at other seasons.

The eggs of each individual (as well as the means of the different individuals) vary less in respect to the dimensional characters than in respect to weight. The eggs must vary simultaneously in both dimensions.

Whereas a comparison of the means for the different individuals shows that intra-racially the eggs are more uniform in yolk weight than in the weight of the other parts or of the whole egg, within the eggs of the individual the yolk weight is almost as variable as the shell weight and much more variable than the weight of the albumen or of the whole egg.

THE RELATION OF EGG CHARACTERS TO OTHER CHARACTERS.

The factors which bring about the individuality in the eggs of the different birds are too complex for analysis from the data in hand. Other facts known about the birds were investigated to discover possible relationships between the variation in egg characters and variation in other characters. The results were as follows:

1. The early hatched birds laid earlier in the fall than those hatched during the middle of the season, while the late hatched birds did not lay until spring.

2. Among the birds which began to lay in the fall there is no relation between the number of eggs laid and the time of hatching or the exact date of the first egg.

3. Among the whole flock there is no relation between the mean size of the egg and either the time of hatching or the time of laying the first egg.

4. Correlations calculated between body weight and number of eggs and size of eggs, and between number of eggs and size of eggs were all significantly zero.

Autopsy data were taken on the thirteen birds which completed their second year. The number of birds is too small for statistical analysis. They show an apparent relationship between the size of the inactive oviduct and the time which has elapsed since the last egg and the amount of yolk present in the ovary. The size of the active oviduct appears to be related to the body size. It is not possible to determine whether or not there is a relationship between the size of the active oviduct and the size of the egg.

THE INTERRELATION OF THE DIMENSIONS, THE SHAPE, SIZE OF EGG AND THE SIZE AND PROPORTION OF THE PARTS.

The individuality of the birds in respect both to the mean size and to the amount of variation of each egg character was discussed in preceding paragraphs. In this discussion it was noted that there was a general relationship between the various characters, that is when an individual laid large eggs her characteristic egg was both long and broad and each one of the component parts was relatively large. It was also noted that the eggs of an individual evidently varied coincidentally in both diametral dimensions since they were less variable in either dimension than in size. It was further noted that within an individual there was a compensatory variation in the size of the parts since the variation in the whole egg is less than the variation in the parts.

The purpose of the present part of the paper is to show the interrelation or more strictly correlation of the various egg characters within the eggs of each of the several individuals.

The results of an analysis of the data may be summarized as follows:

1. Different pairs of egg characters show a decided difference in the degree of correlation.

2. There is a general tendency for a given pair of characters to be similarly related in the eggs of the several individuals.

3. Individuals, however, show significantly different degrees of correlation in any pair of characters. The range of the individual variation is wider and the number of individuals which differ significantly from each other is larger for some pairs of characters than for others.

4. Length and breadth are positively but not highly correlated.

5. Both length and breadth are highly positively correlated with weight.

6. Breadth-weight correlation is as a rule higher than length-weight correlation but an individual may show the reverse relation.

7. Index and weight correlation when significant is negative and low.

8. The relation between length and breadth, length and weight, and index and weight is much closer within the eggs of an individual than within the eggs of the strain, but breadth and weight are as closely related within the eggs of the strain as within the eggs of an individual.

9. In eggs of the same weight the two dimensions are negatively correlated but the degree of correlation varies greatly in the different individuals.

10. Either dimension is highly correlated with weight when the other dimension is constant. The correlation between breadth and weight is higher than the correlation between length and weight. The individual variations are less than in the gross correlations or in the correlations between length and breadth in eggs of the same weight.

11. The weight of each of the three parts of the egg (albumen, yolk and shell) is positively correlated with egg weight. The heaviest part, albumen, is invariably very closely correlated. Yolk is also closely correlated but there is a greater individual variation in the value of the coefficients. Shell, the lightest part, is much less closely correlated and the individual differences are much greater than in the case of the two heavier parts.

12. The correlation between either of the two large parts and the whole egg when the other part remains constant is high and shows insignificant individual differences. The albumen-weight correlation is slightly* higher than the yolk-weight correlation.

13. The correlation between albumen and yolk is higher than the correlation between either of these and shell. In general the albumen shell correlation is higher than that for yolk and shell. The range of correlation for any of these pairs of characters, however, varies in different birds from insignificance to high correlation.

14. In eggs of the same weight any two parts are negatively correlated. The yolk-albumen correlation is highly negative and the different individuals show little variation in the value of the coefficient. The yolk-shell and albumen-shell correlations are significantly negative for most individuals but the value of the coefficients for the different individuals varies greatly.

15. Length and breadth are positively correlated with the weight of each part of the egg. When there is a significant difference between the correlation of length and any part and the correlation of breadth and the same part the breadth correlation is higher.† There is, however, a great deal of individual variation in the degree of these relationships.

16. Albumen and yolk correlations with either dimension are higher than the shell correlation. Albumen correlations are significantly higher than yolk correlations for several individuals. The reverse is true in only one case.

17. In eggs of the same weight the correlation of either dimension with any part is often not significant. The different birds show a great deal of variation in these coefficients. The most usual relationship is for breadth to be positively correlated with yolk and negatively correlated with albumen and shell.

AN ANALYSIS OF THE VARIATION AMONG THE EGGS OF THE SAME BIRD.

It has been shown that while the eggs of an individual resemble each other more closely than do eggs forming a

* This difference may not be significant.

† There are two exceptions to this statement.

random sample from other birds of the same strain, there is nevertheless a high degree of variation among them. This variation is appreciable in every egg character but the several characters show it in decidedly different degrees. The means of the individual coefficients of variation are given in Table 1.

TABLE 1.
Showing the Mean of the Individual Coefficients of Variation for each Egg Character.

EGG CHARACTER.	Mean of the Individual Coefficients of Variation.
Shell weight.....	10.43
Yolk weight.....	9.84
Albumen weight.....	6.43
Egg weight.....	6.36
Length.....	3.32
Breadth.....	2.38

The purpose of the present part of the paper is to investigate further this variation among the eggs of the individual.

The data collected in the present investigation offer material for the study of the following phases of this variation in the eggs of the individual. First the variation due to the age or maturity of the bird, second that due to the seasonal distribution of the laying, third that due to the general physiological conditions, i. e., health of the bird, fourth variation due to the tendency of the birds to lay in litters and fifth that related to the tendency to lay in smaller groups or clutches.

I. THE VARIATION RELATED TO THE AGE AND MATURITY OF THE BIRD.

The data used in this study are the measurements taken on all the eggs laid by each of the twelve birds which lived and continued to lay through two years. To illustrate certain points it is possible to supplement this with the data on the eggs of other birds which did not complete their second year.

The progressive change in egg weight associated with the maturity of the bird is shown by the monthly mean egg weight. In the case of each individual the egg weight at the end of the second year is decidedly greater than at the beginning of the first year. From the beginning of laying until the beginning of the first breeding season the eggs increase rapidly in size. From this time on the weight of the egg is subject to quite perceptible

seasonal fluctuations which will be discussed later; but with very few exceptions the eggs of the second year are decidedly larger than the eggs of the corresponding months of the first year. That is the eggs of a bird continue to increase in weight with the increased maturity of the bird at least up to the end of the second laying year. After the beginning of the first breeding season the increase in weight is much slower than during the few months which precede.

The weight of the egg is made up of the weight of the three parts albumen, yolk and shell. Each of these parts are also variable in weight. In fact, each is more variable than the weight of the whole egg.

A study of the progressive change in each of these parts can be made in a manner similar to the above study of egg weight.

The monthly mean yolk weights show ever more uniformly than the weight of the whole egg that the weight increases rapidly to the beginning of the first breeding season and from that time on more slowly. The yolk weight shows the seasonal fluctuations shown by the egg weight; but their magnitude is smaller.

The monthly mean albumen weights show a less abrupt rise during the first three months and greater seasonal fluctuations than the monthly mean egg weights or yolk weights. In general, however, they show an increase in albumen weight with an increase in the age of the bird.

The monthly mean shell weights are larger for the second than for the first year but they show a large proportional variation which is usually related to the variation shown by the other parts but may be independent and in the opposite direction. For example during the first three months laying all but one of the birds show a decrease in shell weight which is as decided as the increase in the weight of the other two parts.

In order to generalize the study of the increase in the weight of eggs and of each of its parts as the bird grows older it is desirable to bring together the results of the study on the individual birds.

The birds used in this investigation form a more homogeneous group than is often available for statistical work. They were "pure-bred" in the fancier's sense and line-bred and were within a few weeks of the same age. They had lived under the

same environmental conditions since hatching and they began to lay at very nearly the same time. Further there are only slight differences in the degree and direction of variations in the monthly means of the same weight character for the several birds.

The material has been brought together by calculating directly for each weight character the monthly mean of all the eggs laid by the twelve birds.

The means are given in Table 2.

TABLE 2.

Showing for Each Month the Number of Birds Laying, the Number of Eggs Laid and the Mean Egg Weight, Yolk Weight, Albumen Weight and Shell Weight for the Twelve Birds which Completed their Second Year.

MONTH.	No. birds laying.	No. eggs laid.	Mean egg weight, gms.	Mean yolk weight, gms.	Mean albumen weight, gms.	Mean shell weight, gms.	Mean temperature in degrees, F.
1910							
October.....	1	3	48.56	13.66	28.13	6.17	48.40
November.....	12	137	47.48	12.87	29.11	5.46	34.95
December.....	11	206	48.99	13.39	30.38	5.22	19.55
1911							
January.....	12	110	50.37	14.24	30.88	4.84	18.15
February.....	10	100	53.53	16.27	30.94	5.37	14.56
March.....	12	224	54.25	16.18	32.46	5.63	25.20
April.....	12	210	54.42	16.43	32.48	5.54	40.90
May.....	12	192	53.73	16.23	32.12	5.39	59.25
June.....	12	144	53.66	16.25	32.23	5.13	62.30
July.....	11	158	52.22	16.31	30.83	4.87	71.20
August.....	11	170	54.75	16.72	32.53	5.46	66.20
September.....	11	132	55.44	16.88	33.13	5.41	57.20
October.....	9	86	56.68	17.61	33.23	5.55	46.10
November.....	4	15	58.51	17.41	35.57	5.43	34.40
December.....	4	43	59.20	17.50	35.93	5.77	28.00
1912							
January.....	5	29	61.30	17.90	37.72	5.67	10.90
February.....	8	39	54.73	17.85	31.88	5.08	17.70
March.....	11	179	59.03	18.46	34.71	5.68	27.00
April.....	12	130	56.12	17.47	33.10	5.08	43.50
May.....	12	138	55.63	17.71	33.47	5.31	57.10
June.....	11	148	58.10	18.45	34.30	5.62	63.80
July.....	12	137	56.97	18.31	33.46	5.32	67.20
August.....	10	88	57.16	18.16	33.61	5.39	62.50
September.....	11	123	58.46	18.19	34.69	5.53	57.50
October.....	9	83	61.64	18.19	37.20	6.23	49.80

From this table it is seen that in the case of the flock, as in the case of individual birds, the yolk weight increases more constantly than the weight of the other two parts or of the whole egg. That is it shows smaller irregular fluctuations.

The flock monthly mean yolk weight increases very rapidly at first. The increase in weight is actually greater during the first four months than during the next twenty months. The yolk weight, however, continues to increase during the second year. This suggests that the increase in yolk weight is following a logarithmic curve of the form $y=A+Bx+C \log x$ where y =yolk weight, x =time, and A , B and C are constants. This type of curve was fitted as a first trial.

The resulting curve is

$$y=12.6728-.0261x+4.5669 \log x.$$

When the ordinates of this curve are calculated and plotted together with the observation curve the smooth curve shows an excellence of fit which indicates that the increase in weight of the egg yolk in these birds is in fact expressed analytically by this logarithmic curve. In other words this shows that *the mean yolk weight increases with each successive month from the beginning of laying at least to the end of the second year but the rate of increase diminishes with the successive months.*

The data on which these calculations were based were taken from the eggs of birds which began to lay at an age of from five and one-half to six and three-fourths months. It is interesting to know the size of the egg yolks at the beginning of laying and the direction and rate of change in yolk weight when a bird is older or younger than this at the time she begins to lay. For this reason three birds that began to lay February 23 were added to the individuals under investigation. These birds were eight and three-fourths to nine months old, i. e., they were from two to three and one-half months older than those pullets just discussed. It is not so easy to investigate pullets which begin to lay younger, as the Barred Plymouth Rocks, at least under the methods of hatching and handling employed at this station, rarely lay before they are five months old. We are indebted to Mr. Walter Gerald of Unity, Maine, for the opportunity to obtain data on the first ten eggs of a pure bred Barred Plymouth Rock pullet which began to lay when she was exactly three months old and before she had moulted her

chicken feathers. The eggs of Mr. Gerald's pullet were very small and the yolks were only about one-half the size of the yolks of the five to six months old pullets. Also the yolk weight increased considerably during the fifteen days observations.

The case of this precocious pullet adds evidence to the view suggested by the data from the flock investigated, namely that the egg yolks increase in weight as the bird matures and that this increase is more rapid at early than at later stages of development. There is further evidence of this fact from the data on the birds which began to lay in February. These birds were from eight and three-fourths to nine months old when they began to lay.

The relation of the age of the bird at the beginning of laying to the size of the first yolk is shown by the data given in table 3.

TABLE 3.
Showing the Relation of the Age of the Bird to the Size of the 1st Yolk.

BIRD No.	Age at laying 1st egg.	Weight of 1st yolk.	Mean.
Mr. Gerald's pullet,	3	6.21	6.21 (1 bird).
218	5 $\frac{1}{2}$	10.19	10.945 (4 birds).
516	5 $\frac{3}{4}$	10.75	
478	5 $\frac{3}{4}$	9.30	
236	5 $\frac{3}{4}$	13.74	
446	6	13.09	12.236 (13 birds).
184	6	12.22	
441	6	12.63	
259	6 $\frac{1}{4}$	10.68	
212	6 $\frac{1}{4}$	11.74	
235	6 $\frac{1}{4}$	14.05	
192	6 $\frac{1}{4}$	10.51	
204	6 $\frac{1}{2}$	12.27	
198	6 $\frac{1}{2}$	11.53	
139	6 $\frac{3}{4}$	11.51	
211	6 $\frac{3}{4}$	12.28	
205	6 $\frac{3}{4}$	13.22	
243	6 $\frac{3}{4}$	13.35	
137	7	13.75	13.51 (2 birds).
172	7 $\frac{1}{4}$	13.27	
459	8 $\frac{3}{4}$	14.19	15.643 (3 birds).
489	8 $\frac{3}{4}$	17.63	
514	9	15.11	

Data on the eggs of the birds which began to lay in February show also that in these cases the yolk weight does not begin small and increase very rapidly, as in the case of the birds which begin to lay in the fall. In fact with one exception the yolk weight shows a slight decrease for the first few months.

This is evidently a seasonal decrease as it is shown by several of the birds that began to lay in November. Unfortunately none of these birds laid through the second year but up to within a month of death these birds showed monthly means very similar to the means for others of the flock during the same months.

Another bird (No. 236) laid one egg in November but did not lay again until March 31. She may therefore be considered as a bird without laying experience until she was practically nine and three-fourths months old. The one egg in November however indicates the size of eggs she would have laid at that period.

A comparison of the monthly mean yolk weight for these four birds with those for the other birds of the flock shows that the first eggs laid by birds which do not lay until they are nine months old have yolks as large as the yolks of the eggs laid at the same time by birds of practically the same age which began to lay some months earlier. The rate of change in yolk weight also is similar to that shown during the same time by the birds which had laid younger. The one observation in November for bird No. 236 is also in accord with the observations for the other birds at that time.

It is also interesting to note that the yolk weights shown by any bird at any month are dependent upon the size typical for the individual and upon the time of year. It is apparently independent of whether the bird has been laying during the previous months, or, in fact, of whether or not she has ever laid before. *That is the increase in yolk weight does not seem to be due to a perfection of the morphogenetic activity due to physiological practice but seems rather to be due to the stage of development or differentiation of the individual.*

Since the birds used in this investigation were very nearly the same age it is not possible to separate absolutely the effects of the age of the bird and of the season of the year. Certain undoubted seasonal variations will be discussed later. It seems however that the general tendency for a continued increase in yolk weight at a constantly diminishing rate through all seasonal conditions must be due to the general stage of maturity of the bird. The small but rapidly increasing yolks in the precocious pullet also supports this view. This gradually diminishing increase in yolk weight is represented by a logarithmic

curve. This curve which represents analytically the law of the increase in yolk weight with the age of the bird is of the same type as the curves which have been found to fit various kinds of growth data in both animals and plants.

The first interpretation that suggests itself is that this increase in the size of the yolk is a direct effect of the analogous increase in the size of the individual. That the body weight as well as yolk weight normally continues to increase at least to the end of the second year was seen by comparing the body weights at the beginning, middle and end of the observations. However, the curve showing the increase in yolk weight is not parallel to a curve which shows the increase in body weight at the same period. During the period of most rapid increase in yolk weight the increase in body weight was too small to be certainly distinguished from the fluctuations due to temporary variations in the amount of food and waste present in the body. This indicates that *the stage of development or differentiation which determines the size of yolk is not accurately measured by the body weight*. It is of course well known that the different organ systems of the body show different growth stages at the same time and that the reproductive system shows most rapid growth not long before the beginning of its functional activity.

In yolk weight we find a logarithmic approach of successively formed structures to a type. Pearl* ('07) found this true of leaf number per whorl in *Ceratophyllum* and later ('09)† of egg shape in a domestic fowl. *In the case of yolk weight, however, it is certain that this is not due to the continued production of the like parts but to the condition of the individual at the time the part is produced.*

The change in yolk weight due to the age or maturity of the bird has been discussed at length because the weight of this part of the egg seems to be most closely related to the age of the bird and least affected by the other natural causes of variation in egg size. The weight of albumen and shell also both

* Pearl, R., Pepper, O. M. and Hagle, F. H. Variation and Differentiation in *Ceratophyllum*, Carnegie Institution Publ. No. 58, pp. 1-136. 1907.

† Pearl, R. Regulations in the Morphogenetic Activity of the Oviduct. Jour. Exp. Zool., Vol. VI, 1909, pp. 339-358.

increase with the age of the bird but the fluctuations are much greater than in the case of yolk weight. Since the weight of each of the parts increases with the age of the bird the weight of the egg must show this relation also. In the case of the yolk weight we have seen that the rate of increase is quite precisely logarithmic. The fluctuations from this type are small. Albumen weight shows a tendency to this type of increase but certain fluctuations are very great. The increase in shell weight is not logarithmic. The weight of the whole egg shows an increase in weight distinctly logarithmic although less precisely so than yolk weight.

The different nature of the physiological processes involved in the formation of the parts of the egg affords ample basis for an independent variation. The weight of the yolk is determined by the amount of yolk deposited while it is within the ovarian follicle. The albumen weight depends upon the amount of secretion of the albumen glands of the entire oviduct, while the weight of shell depends only upon the secretions of the shell forming glands of the uterus. It is conceivable that a disturbance of the processes involved in the formation of one part of the egg may have little or no effect on the processes involved in the formation of the other parts. The results given above indicate that the factors which determine the size of the yolk are less disturbed by temporary conditions than are those which determine the amount of albumen and shell secretion.

2. VARIATION RELATED TO THE SEASON OF THE YEAR.

Yolk weight and albumen weight show in general similar seasonal variations. Both parts increase in weight from the beginning of the fall laying to the beginning of the breeding season in February or March. This increase is proportionately greater in albumen weight than in yolk weight. At the beginning of the breeding season the yolk weight increases while the albumen weight either remains constant or decreases. The yolk weight remains nearly constant during the breeding season and the following summer, but the albumen weight tends to fall off especially as the molt is approached. Thus the proportion of yolk in the eggs during the spring and summer is larger than during the fall and early winter.

When the monthly mean shell weight is compared month by month with the monthly mean albumen weight many of the same fluctuations will be noted. There is one decided exception. During the first three months shell weight is decreasing proportionately more rapidly than the albumen weight is increasing. The fluctuations shown at other seasons are proportionately much greater in shell weight than in albumen weight.

The variation in weight which is associated with the change in season is to a certain extent similar in the case of each part of the egg. The parts, however, vary greatly in the proportional magnitude of the seasonal variations. The difference is so great that the proportion of the parts is altered in different seasons. *Yolk weight is apparently least affected by these seasonal factors. Albumen weight shows very large fluctuations which have a decided tendency to repeat themselves in successive years and therefore appear to be undoubted seasonal fluctuations. The fluctuations in shell weight are proportionately greater than in either of the other parts, but do not show the same tendency to repeat themselves in the successive years. It therefore seems possible that some of the large fluctuations in shell weight may be due to some other circumstances than the normal change in season.*

Showing that certain changes in yolk weight and albumen weight are correlated with change in season does not indicate the fundamental cause of these changes. The solution of this problem must be by controlled experiments. Two interpretations suggest themselves. 1. The fluctuations may be due to the direct effect of seasonal changes in environment. 2. They may be due to the general changes in metabolic processes which also find expression in the differentiation of a breeding season and a fall molt, and which are probably due in part to environment and in part to heredity.

In general it seems probable that while the seasonal fluctuations in egg weight may be to some extent the direct effect of environmental conditions, yet to a much greater extent they are the indirect effect of such conditions. That is they are due to general physiological changes in the individual.

3. VARIATION RELATED TO THE STATE OF HEALTH.

One of the birds (No. 441) used in this investigation offers an opportunity to study the effect of the state of health upon the weight of the egg. This bird laid 179 eggs during her pullet year. These eggs increased in size exactly in accordance with the general rule for the flock. Her body weight increased from 2003 gms. in November and December 1910 to 2325 gms. in September, 1911. That is up to the first fall month she was a normal bird. She stopped laying for the molt October 17, 1911, and did not lay again until March 4, 1912. From this time until August 17 she laid quite well for a second year Barred Plymouth Rock, producing 90 eggs in this time. These eggs were smaller than the eggs of the previous year. Nothing abnormal was seen in the appearance of the bird until during the summer when she began to appear somewhat sick. She continued to lay until August 17. After this she became more dumpish. In September it was apparent that she would not recover and lay before the close of the investigation in November. She was therefore, killed and autopsied September 10, 1912.

At autopsy her body weight was 2190 gms., a slight decrease from the weight a year before. The following lesions were recorded: 1. The liver was congested and friable. 2. The lungs were congested and showed yellowish lesions. 3. There was some peritoneal disturbance which had caused a greenish deposit on the intestinal mesentery. That is the bird at autopsy showed evidences of disturbances which were probably of some time standing.

A comparison of the egg data for this bird with the corresponding data for the other birds show that during the first year each egg part increased in weight in the normal manner. The bird was then no doubt in good physical condition. The bird did not lay from October, 1911 to March, 1912. Throughout the second year the weight of each egg part decreased. This decrease was most rapid after the bird was observed to be sick but had been going on for three months before this. Evidently the physiological disturbances had affected the size of the egg before they affected the behavior of the bird.

Five other birds died or were killed during the investigation.

None of these were affected by long standing diseases and none showed a diminution in egg size greater than normal variation.

It is clear that a diseased condition of a bird may cause a decrease in the weight of each part of the egg without causing a cessation of laying. It is also clear that other disturbances sufficient to cause death may not affect the size of the egg produced on the day of death.

Féré* studied the effect of morphine intoxication on the weight of the egg. He found that a stupefying dose caused a diminution in the weight of the egg which was laid on the day of the intoxication and which must have been nearly formed at the time of the injection of the morphine.

The effect of the morphine interrupted the laying for four days and when it was resumed the first two or three eggs were smaller than before the intoxication. This shows that an experimentally altered physiological condition may cause a diminution in the weight of the egg.

It has been shown that, in general, the monthly mean egg weight increases with the age of the bird, fluctuates with the season of the year and is affected by the state of health. The fact now to be considered is that during any month the eggs of each bird show a very considerable variation in egg weight and in the weight of each of the egg parts.

Before considering the nature of this variation in the weight of the successive eggs it is important to notice the following points in regard to the rate of production of the bird.

1. Periods of production alternate with periods of non-production. That is the bird lays in litters.
2. The length of the periods of production and the number of eggs laid in one litter vary at different seasons of the year.
3. Throughout the warm months (April to September) the period of non-production is typically a period of broodiness. That is the instinct of the bird is to lay a litter of eggs and then incubate them. While thirteen of the birds show this instinct, nine were never broody. It is also interesting that broodiness or non-broodiness is typical of the individual, for

* Féré, M. Ch. Note sur la puissance toxique et la puissance tératogène de la morphine sur le poulet. Bull. et mém. de la Soc. méd. des hop. de Paris, Vol. 14, séries 3, pp. 608-617, 1897.

when a bird was broody the first year she was also broody the second year and if she was not broody the first year she did not show this instinct the second year. Typically a bird which was broody at all was broody four or five times during a season but the number of times varied from 1 to 7 with the individual. The nine birds which were never broody show all degrees of a tendency to lay in litters from zero in the extreme case of one bird which laid from February to the end of the year at a nearly uniform rate, i. e., in clutches of 1 to 3 usually two eggs separated by one or two days on which no egg was laid, to the opposite extreme of a bird which had exactly the same definite periods of non-production as the birds with typical broody periods but she lacked the instinct to incubate the eggs.

4. Within a litter the laying is broken up into clutches. The eggs of a clutch are laid on successive days. The clutches are separated by one or two (occasionally more) days on which no eggs are produced.

5. The number of eggs in a clutch and the number of days between clutches vary in the different birds in the same season and in the same bird at different seasons. During the part of the year when the bird is not laying in litters succeeded by broody periods the size of the clutches is small. The birds which lay continuously (i. e., do not lay in litters) lay in small clutches throughout the season. During the part of the year when periods of production alternate with periods of broodiness the litters show a decided tendency to start and end with small clutches while the number of eggs in the intermediate clutches is larger. An individual may nevertheless start or end a litter with large clutches.

These facts, in general, accord with the hypothesis of Pearl and Surface.* "The actual visible egg production in each individual bird tends to occur in definite cycles or periods of varying lengths, alternating with non-productive periods."

"The rate of fecundity (amount of egg production per unit of time conceived in the sense of the differential calculus) is in any bird a minimum at the beginning of the cycle of produc-

* Pearl, R. and Surface, F. M. A Biometrical Study of Egg Production in the Domestic Fowl. II. Seasonal Distribution of Egg Production. U. S. Dept. of Agr., Bul. An. Ind. Bul. 110, Pt. II, 1911.

tion, increases to a maximum at what may be termed the height of the cycle, and decreases to a minimum as the end of the cycle is approached."

In order to make a study of the variation in the physical characters of the successive eggs of an individual in relation to the variation in her rate of production, the weight of each egg and of each of its parts was plotted as ordinate and the date of laying as abscissa. Such diagrams were made for each bird. A study of these shows the relation of the weight of the egg and of each egg part to its position within the clutch and litter.

4. RELATION OF THE WEIGHT OF THE EGG TO ITS POSITION IN LITTER.

Féré's † statement that, in general, the eggs at either end of the litter are smaller than the intermediate ones but that this relation is not absolute is verified by the observations on the birds used in the present investigation. In fact the weight of the egg in relation to the position within the litter approximates a curve of the type of the hypothetical "rate of fecundity" curve proposed by Pearl and Surface ‡ (1911). It thus seems possible that the same conditions which cause fluctuations in the rate of production may also be responsible for the cyclic fluctuation in the egg weight. It is certain, however, that the weight of the egg is also related to the position of the egg in the clutch and that the position of the egg in the clutch and in the litter may have opposite effects on the size.

5. RELATION OF WEIGHT OF THE EGG TO ITS POSITION IN THE CLUTCH.

When an egg was produced on each day for a number of successive days, as a rule, the eggs decreased in weight from the first egg to the end of the series. The first egg after a day on which no egg was laid was larger than the egg at the end of the preceding series. That is the eggs of the clutch decrease

† Féré, M. Ch. Note sur le poids l'oeuf de poule et sur variation dans les pontes successives. *Journal de l'Anatomie et de la Physiologie*. T. 34, pp. 123-127, 1898.

‡ Pearl and Surface. *Loc. cit.*

in size from the first egg. The first egg of a new clutch is larger than the last egg of the preceding clutch. There are a few exceptions to this especially where a litter begins with a long clutch.

The fact that in general the eggs laid on successive days decrease in size while after a day or two on which no egg is produced the egg size increases seems to indicate that there is either an exhaustion of material available to elaborate into the various egg parts or that there is a fatigue of the reproductive organs which causes a decrease in the amount of material elaborated. A variation in the supply of available materials or a variation in the physiological tone of the organ would account for the cases of unusual size relations between successive eggs.

It has now been shown that the variation in egg weight is related to the age of the bird, the season of the year, the state of health and the rate of egg production.

The weight of all the eggs and egg parts for the individual birds for two years furnish material to test Pearl's* ('07) "second law of growth" i. e., that the variability of successively produced like parts decreases with the number of such parts produced. If this law was operating during the production of successive eggs the magnitude of the fluctuations in egg weight would decrease with the number of eggs laid. The diagrams described on page 125 show that the fluctuations in egg weight and weight of each of the egg parts are as large at the end of the second as at the beginning of the first year. It is evident then that this law does not hold for the variation in weight of successive eggs. Pearl† ('09) found no evidence that this law was acting in regard to the shape of the eggs of a fowl on which he studied regulation in shape.

This section of the paper has shown that *the weight of any part of a bird's egg depends, first upon the hereditary constitution of the bird, second her physical constitution or state of health, third, her stage of development, fourth, the season of the year, and fifth, the position of the egg in its clutch and*

* Pearl, R. *Loc. cit.*

† Pearl, R. *Loc. cit.*

litter. It has also shown that *the variation in successive eggs is as great at the end of the second as at the beginning of the first year's laying*.

DISCUSSION OF RESULTS.

Only a beginning of the analysis of the factors which produce variation in the eggs of the domestic fowl is possible from the results of this investigation.

Since the individual variation in egg characters is less than race variation, and since the association of various pairs of egg characters is greater within the egg of an individual than within the eggs of the race, it is concluded that an individual inherits or, at least, possesses at sexual maturity, the tendency to lay eggs of a certain particular and individual shape, size and physical constitution.

The seasonal and cyclic fluctuations in the eggs of the individual on the other hand show that this predisposition toward eggs of a particular type and size may be influenced by physiological and possibly also environmental conditions.

That the individuality in egg characters is related to individuality in other characters seems certain. The fact that the large varieties of hens lay larger eggs than bantams indicates that within broad limits the size of the egg is related to body size. The insignificance of the correlation coefficient between egg size and body size for the egg of the individuals studied however shows that this relation does not necessarily obtain within narrow limits. It is not possible to decide the limits of the relation of body size to egg size from so small a number of individuals. The point is open to further investigation.

In the study of egg characters it must be kept in mind that eggs are quite different material than is usually employed in biological studies of variation. They are not organs or parts of organs that owe their size and shape to growth, i. e., the proliferation of the cells of which they are made up. Each egg is one modified cell and represents the accumulated results of the activity of a great many cells, not a part of it. The different parts of the egg arise from different organs or parts of organs (the ovary and the parts of the oviduct) and by quite distinct physiological processes (yolk deposition and albumen, membrane, and shell secretion.)

The egg then represents not a normal organic part of the individual but a discrete unit of production of certain correlated organs. The size and form of such units are to a certain extent dependent upon the size and form of these organs. But the size, form and frequency are necessarily also dependent upon the physiological tone of the organs and of the entire organism.

It is not strange that the same individual at different seasons and different individuals throughout the year may show variations in egg size and in the number of eggs produced which are out of proportion to the variation in body size. It is quite possible that egg production like milk production* is related to the amount of food consumed above maintenance. That is the bird which lays large eggs and many of them is one which in addition to the organic potentiality to lay eggs of this size possesses also both the physiological capabilities of digesting a large amount of food above the amount required for the maintenance of the body and of using this absorbed food for the production of yolk, albumen, etc. The fact that the same individual lays larger eggs and more of them at certain seasons than at others may be due to the fact that she is capable of digesting and utilizing for egg production more food at those seasons. It has in fact been shown by Rice** that the number of eggs produced by a flock is positively correlated with the amount of food consumed, and the fluctuations which he found characteristic for the amount of food consumed are very similar to the seasonal fluctuation in egg weight. The work of Riddle† on yolk formation also supports this view.

In general the conditions which favor the production of a large number of eggs also favor the production of large eggs (i. e., large for the particular individual). Yet there are

* Eckles, C. H., and Reed, O. E. A Study of the Cause of Wide Variation in Milk Production in Dairy Cows. Mo. Agr. Expt. Sta. Research Bul. No. 2, 1910, pp. 107-147.

** Rice, J. E. The Moulting of Fowls. Cornell Univ. Exp. Sta. Bul. 258, 1908, pp. 21-68.

† Riddle, Oscar. On the Formation Significance and Chemistry of White and Yellow Yolk of Ova. Journal of Morphology, Vol. 22, 1911, pp. 456-484.

limits to this relationship. When a number of eggs are produced in succession each successive egg is smaller than its predecessor. There is probably either an overdemand on the amount of available material or there is a fatigue of the reproductive apparatus which hinders the formation of the egg parts.

A study of the interrelation of the different parts of the egg is a study of the correlation of the activities of the different organs and parts of organs by which they are formed. The fact that the oviduct of a bird approaching a period of laying enlarges as the yolks enlarge has been long recognized. The observations on the domestic fowl at this laboratory agree in general with those of Bartelmez* on pigeons. There are nevertheless some specific differences between fowls and pigeons. In a bird in the non-laying condition the oviduct is a small straight tube and there are no oocytes in the ovary which contain a perceptible amount of yolk. About the time a group of oocytes enters upon the final growth period (when they begin to enlarge above 6 mm.) the oviduct begins to enlarge. The stimulus which initiates these activities in fowls is not known. There is no evidence that it is connected with mating as has been shown for the pigeon.† The presence of the male is certainly not necessary and no behavior on the part of a fowl has been observed to indicate that she is physically mated with another female or with anything else. Whatever the stimulus that starts the reproductive mechanism going, it is true that while the first yolk is forming the oviduct enlarges to functional size.

This correlation between the ovary and oviduct is now commonly attributed to the action of the internal secretion of the ovary. Bartelmez‡ states that "interstitial cells of the ovary show much greater signs of activity in functioning ovaries than do those in ovaries of birds that had not laid for a long time." That the enlargement of the oviduct is due to the in-

* Bartelmez, George W. The Bilaterality of the Pigeon's Egg. Jour. of Morph., Vol. 23, 1912, pp. 270-310.

† Harper, E. H. The Fertilization and Early Development of the Pigeon's Egg. Am Jour. Anat., Vol. 3, 1904, pp. 344-381.

Craig, W. Oviposition Induced by the Male in Pigeons. Jour. of Morph., Vol. 22, 1911, pp. 299-305.

‡ Bartelmez, G. W. *Loc. cit.*

ternal secretion of the ovary has not been completely demonstrated by any means. Certain observations made in connection with other researches make the conclusion somewhat doubtful. They certainly show that enlargement of the oviduct is not necessarily connected with yolk formation although this is the normal relation.

The observations referred to are:

1. The oviduct of the hermaphrodite fowl described by Pearl and Curtis* was at autopsy in essentially the same condition as that of a normal fowl that had recently completed or was soon to begin an egg laying period. Yet this bird had never laid and the histological examination of the ovary failed to demonstrate the presence of oocytes in any stage of development. The ovary of this bird was about the size of a functioning ovary after the large yolks have been removed. It was composed of a highly cellular stroma like tissue penetrated from the stalk by a very vascular connective tissue and covered externally by a layer of peritoneum. The presence of interstitial cells could not be demonstrated, but this may have been due to poor fixation.†

2. In the routine autopsy work in this laboratory there has been noted several cases of birds which had not laid for a long time and which had no oocytes with any yolk but which possessed nearly functional sized oviducts. There were in these cases ovarian tumors which seemed here to be associated with the enlarged oviducts. None of these ovaries were examined for interstitial cells which may or may not have been present.

That the mere increase in weight of the ovary may stimulate the enlargement of the oviduct is not altogether impossible. These pathological ovaries may however have furnished the normal internal secretion in quantities sufficient to cause the enlargement of the oviduct. It is nevertheless certain that whatever the stimulus may be it is not absolutely dependent

* Pearl, E., and Curtis, M. R. Studies in the Physiology of Reproduction of the Domestic Fowl. A Case of Incomplete Hermaphroditism. Biol. Bul., Vol. XVII, pp. 271-286, 1909.

† The whole reproductive apparatus and the dorsal part of the body was preserved in formalin and dissected for anatomical study. The histological sections of this formalin tissue showed rather poor fixation.

upon the deposition of yolk. The teleological view that the oviduct enlarges in order to be ready to lay the first egg is not tenable. Normally the oviduct enlarges while the yolks enlarge and reaches functional efficiency by the time the first yolk is mature.

The stimuli which initiate the peristaltic action of the oviduct and attract the funnel to the mature follicle are among the unsolved problems of physiology. The yolk is already oriented in the follicle before the funnel encloses it. In pigeons* both chalazal and polar axes are determined in the primordial follicle; the first by the long axis of the oocyte and the second by the eccentric germinal vesicle. The polar orientation of the egg in the follicle is due to the action of gravity after the yolk becomes movable in the follicle (at the time of the formation of the zona radiata). The vegetative pole is heavier than the animal pole, hence the animal pole comes to lie beneath the stalk of the follicle.

Due to the pressure of the inclosing funnel and to increased internal pressure, the yolk ruptures the follicle and becomes free in the duct. At this time the secreting activity of the duct begins. Again the precise nature of the stimulus is not certainly known. It is normally connected with the presence of the yolk; but albumen secretion followed by normal membrane and shell formation have been induced in functioning oviducts by the insertion of artificial yolks. Results of this kind are reported by Weidenfeld† and Tarchanoff‡. Unpublished investigations at this laboratory have also shown that an egg may be formed around an artificial yolk or the artificial yolk may be fastened in the upper part of the oviduct and an egg may be formed which contains chalazae, both kinds of albumen, normal membrane and shell. This last result as well as the not infrequent occurrence of small yolkless eggs which contain all the other normal egg parts show that the secretory process may

* Bartelmez, G. W. *Loc. cit.*

† Weidenfeld. *Verh. der Ornithol. Gesellschaft, Bayern*, 1905, p. 112.

‡ Tarchanoff, J. R. Ueber die Verschiedenheiten des Eiereiweisses bei befiedert geborenen (Nestfluchter) und bei nackt geborenen (Nesthocker) Vögeln und über die Verhältnisse zwischen dem Dotter und dem Eiereiweiss. *Pflüger Archiv für Physiologie*, Vol. 33, 1884.

be started off by some adequate stimulus (probably in the case of the yolkless eggs by the presence of a yolk in the oviduct which is later expelled into the body cavity) and may then continue to completion without the presence of the yolk. These results with artificial yolks indicate that the stimulus may be mechanical but the experiments of Tarchanoff § and unpublished work done in this laboratory also show that an egg is not always formed around an artificial yolk introduced into an oviduct which is in functional condition. Until the other conditions necessary for the formation of eggs with artificial yolks are determined it cannot be certainly said that the only stimulus necessary is mechanical.

That the amount of albumen secretion of the oviduct is related to the degree of the stimulation by the yolk is shown by the significant correlation between the weight of the yolk and the weight of the albumen. Since the secretion of the duct does not begin until the yolk has completed its growth and severed its connection with its follicle this seems to be the only possible explanation of the correlation. To this evidence that the degree of stimulation influences the amount of secretion may be added that from abnormal eggs which contain unusual large or small quantities of yolk. On the one hand are the double and triple yolked eggs and on the other the "cock-eggs" or "witch-eggs" which contain little or no yolk. Pearl* ('10) showed that "the relation of the observed size of the entire egg (measured here by the weight) to the number of yolks is very accurately described by a parabola." He pointed out that this indicated that the amount of albumen secreted was related to the amount of the immediate mechanical stimulation due to the quantity of yolk present in the oviduct.

The formation of the egg membrane is a discrete process. As an egg passes from the albumen portion into the isthmus as much of it as is within the isthmus is covered with mem-

§ Tarchanoff, J. R. *Loc. cit.*

* Pearl, R. A Triple Yolked Egg. *Zoölogischer Anzeiger*, Bd. XXXV, pp. 418-423, 1910.

† Coste, M. *Histoire du développement des corps organisés*. Paris, 1874.

brane.† The membrane becomes thicker during the passage through the isthmus‡ probably by the addition of successive layers of secretion.

When the egg enters the uterus it is enclosed in a firm tough membrane and is often if not always already shaped. It contains the yolk with chalazae and 60 to 70 percent of its albumen.§

Within the uterus the egg receives the rest of its albumen (by osmosis) and its shell. The nature of the stimulus which sets up the shell secreting activity was investigated by Pearl and Surface.* The conclusions from their preliminary experiments were that the nature of the immediate stimulus which sets the shell secreting activity going in an oviduct in active functional condition is mechanical, and that shell formation is a local reflex not immediately dependent upon a specific activity of other portions of the reproductive apparatus.

That the weight of the shell is significantly correlated with the weight of each of the other parts indicates that the amount of secretion is influenced by the degree of stimulation. The larger the egg the greater the mechanical stimulation and hence the heavier the shell. The higher correlation between albumen and shell than between yolk and shell is probably due almost entirely to the fact that the albumen is heavier than the yolk. It may be partly due to the fact that 30 to 40 percent of the albumen is secreted in the uterus and that the periods of the albumen secretion and shell secretion overlap although the former is evidently complete before the latter has advanced very far.†

Abnormally thin shelled eggs are as likely to be large as small and no doubt represent either a premature expulsion of the egg or an early arrest of the shell secreting activity.

‡ Pearl and Curtis. Studies in the Physiology of Reproduction of the Domestic Fowl. V. Data Regarding the Physiology of the Oviduct. Jour. Exp. Zool., Vol. 12, 1912, pp. 99-124.

Membranes on eggs just completely past the cranial end of the isthmus weigh .24 to .28 grams. Those at the caudal end .53 to .58 grams.

§ Pearl and Curtis. *Loc. cit.*

* Pearl, R. and Surface, F. M. Science, N. S., Vol. XXIX, pp. 428-429, 1909.

† Pearl and Curtis. *Loc. cit.*

The shape of the egg is almost certainly due to the interaction of the two layers of muscle fibers in the oviduct walls.[‡] The inner layers of fibers is circular, that is they pass around the duct. The outer layer is longitudinal and somewhat spiral and extends into both the dorsal and ventral ligaments. Further work on the physiology of these muscles is necessary to determine the exact way in which they act. From their position and from observed activities of the duct it seems that the contraction of the circular fibers contract the duct and move the egg forward. The contraction of the longitudinal fibers, which have a somewhat spiral course, expand the duct, diminishing the resistance to the passage and also give the egg the spiral motion. If the resistance is slight, i. e., if the contractions are so timed that the duct ahead of the egg is expanded at the time of the contraction of the circular fibers behind, the egg will be long, narrow and pointed. On the other hand, if the resistance is great the egg will be short and broad.

The individuality of the eggs of a bird in respect to shape must be due to an individuality in the coördination of these two sets of muscle fibers and similarly the variation must be due to a variation under different conditions in the degree of coördination.

Breadth is more closely correlated with weight of the whole egg or with the weight of any of the parts than is length. This may be explained by the assumption that the larger the egg (beginning with the yolk) the greater the resistance to its passage and hence the broader it will be in proportion to the actual weight. This may be simply the mechanical effect of a larger body passing through the elastic tube or it may be due to an unequal increase in the effective stimulation of the two sets of muscle fibers.

GENERAL SUMMARY.

This paper is an analysis of the normal variations in the size, shape, and physical constitution of the eggs of the domestic

[‡]Curtis, M. R. The Ligaments of the Oviduct of the Domestic Fowl. Ann. Rept. Me. Agr. Expt. Sta., 1910, pp. 1-20.

Surface, F. M. The Histology of the Oviduct of the Domestic Hen. Ann. Rept. Me. Agr. Expt. Sta., 1912, pp. 395-430.

fowl. The data on which it is based are the measurements of all of the eggs laid by twenty-two Barred Plymouth Rock birds. For thirteen of these birds records were taken on every egg laid up to the end of the second laying year. For the remainder records were taken covering the eggs of the first laying year. The thirteen birds which were alive at the beginning of their second adult molt were killed at that time. The more important results of the investigation may be summarized as follows:

I. *The Individuality of the Eggs of the Same Bird.*

1. The individuality of a bird is expressed in each physical character of her eggs.

2. This individuality is more pronounced in respect to the size than the shape of eggs and also in respect to the weight of albumen and shell than weight of yolk.

3. There is a tendency for the several egg characters to be related to each other in such a way that when the eggs of an individual are large they are both long and broad and each of the parts is large; but the hens which lay large eggs lay eggs with a smaller proportion of yolk than hens which lay small eggs. Also individuals may show a decided tendency to vary from the flock type in quite different degrees in different characters.

4. The eggs of an individual tend to be either uniform or variable in all the egg characters but certain individuals may be variable in certain egg characters and uniform in others.

5. An individual is in general less variable than the race in respect to egg characters; but certain individuals may show a variation in an egg character which is relatively as great as the variation in the race. Also certain egg characters (particularly yolk weight) show a decided tendency to approach the race variation in several individuals.

6. The factors which bring about the individuality in respect to egg characters are too complex for analysis from the data at hand.

II. *Correlation of Egg Characters.*

1. Each egg character is related to every other egg character, but different pairs of characters show a decidedly differ-

ent degree of correlation. There is a general tendency for a given pair of characters to be similarly related in the eggs of the several individuals, but different individuals may show significantly different degrees of correlation in any pair of characters.

2. Length and breadth are significantly but not highly correlated. Both length and breadth are significantly correlated with the weight of the whole egg and of each of the egg parts. Breadth is as a rule more highly correlated with these weight characters than is length. The shape of the egg as measured by the length-breadth index is negatively correlated with the weight of the egg and with the weight of each of the egg parts.

3. The weight of each part of the egg is positively correlated with the weight of both the other parts.

III. *Intra-individual Variation.*

1. The variation among the eggs of the same bird is shown to be related to certain other changes in the bird.

2. The egg weight and the weight of the egg parts, especially the weight of the yolk, increases as the bird matures. The rate of this gain in weight decreases with the successive months.

3. Each part of the egg shows a seasonal fluctuation in weight which is apparently related to the general seasonal fluctuation in the physiological activities of the bird, expressed also in the curves for food consumption and egg production.

4. The state of health also may affect the size of the egg.

5. The size of the egg is related to the rate of production as it expresses itself in the laying of litters. As a rule the first and last eggs of a litter are smaller than the intermediate ones.

6. When eggs are produced on successive days they tend to decrease in weight while the egg laid on a day after one on which no egg is produced is larger than the last egg of the preceding series.

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Curtis, M.R.
Factors influencing
the size, shape and
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